From Bottleneck to Breakthrough: Urbanization and the Future of Biodiversity Conservation

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For the first time in the Anthropocene, the global demographic and economic trends that have resulted in unprecedented destruction of the environment are now creating the necessary conditions for a possible renaissance of nature. Drawing reasonable inferences from current patterns, we can predict that 100 years from now, the Earth could be inhabited by between 6 and 8 billion people, with very few remaining in extreme poverty, most living in towns and cities, and nearly all participating in a technologically driven, interconnected market economy. Building on the scholarship of others in demography, economics, sociology, and conservation biology, here, we articulate a theory of social–environmental change that describes the simultaneous and interacting effects of urban lifestyles on fertility, poverty alleviation, and ideation. By recognizing the shifting dynamics of these macrodrivers, conservation practice has the potential to transform itself from a discipline managing declines ("bottleneck") to a transformative movement of recovery ("breakthrough").

Keywords: demographic transition, poverty alleviation, cities, natural resources, consumption

> In casting up this dread balance-sheet, contemplating our dangers with a disillusioned eye, I see great reason for intense vigilance and exertion, but none whatever for panic or despair.
>
> (Winston Churchill, *Speech to the House of Commons*, 18 June 1940)

The global conservation movement is little more than a century old and, throughout its life, has displayed a consistent and defining characteristic: a brave and worthy but often futile struggle against the forces of growing human consumption, typified by persistent and widespread declines in species' populations, habitats, and natural resources, and the rising specter of climate change. The Global Biodiversity Outlook 4 (CBD 2014), while finding some improvements in temperate and developed parts of the world and the ongoing enlargement of the protected-area estate, also presented evidence of climate-induced effects on biodiversity; the increased spread of diseases and invasive biota; declines in species living in forests, reefs, and many other habitats; and the conversion of ecosystems supporting many kinds of life to ones with singular human uses. In combination, these factors are driving the loss of biodiversity and ecosystem function on a global scale.

Some authors see in these trends threats not just to other species but also to the "safe operating space" for humanity as the Earth nears or exceeds "planetary boundaries" (Rockström et al. 2009). In this vein, Steffen and colleagues (2011) showed 12 plots of growth in the human population and economy paired with 12 plots showing dramatic growth in the amount of disturbance to natural processes caused by human activity. Each graph shared the same *x*-axis, from 1750 to 2000. They suggested that 1800 marks the approximate beginning of the "Anthropocene" age on Earth and that the end of World War II marks a "Great Acceleration" brought on by growth in human population, urbanization, and expansion of the economy.

The Great Acceleration, Steffen and colleagues (2011) argue, is at the root of the environmental crises of our time. Their work builds rhetorically on modern foundations laid by Paul Ehrlich (1968) in *The Population Bomb* and carried forward by many others over decades (e.g., Wackernagel and Rees 1996, Sanderson et al. 2002, Meadows et al. 2004, Rockström et al. 2009). These authors repeatedly make the same point: that the human population, through affluence (which translates into consumption) and facilitated by technology, is damaging the natural bases of life on Earth. Ehrlich and Holdren (1972) formulated the *IPAT relationship*, which states, to a first approximation, that environmental impact

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is the product of population, affluence, and technology ($I=P^*A^*T$). With the global population and rates of per capita consumption increasing since the 1950s (indeed, since the 1750s), environmental impacts have mounted to ever greater and unprecedented extremes (McNeill 2001).

In response to this harrowing view of environmental history, many twenty-first-century conservationists have succumbed to jeremiad, bickering, and despair. Bleak prognoses about the future abound (e.g., Visconti et al. 2016), casting conservation as an unremittingly dire discipline fading into political irrelevancy (Shellenberger and Nordhaus 2004). Recently, some have argued that rather than opposing the forces of economic development, "new" conservation must join them, with a renewed focus on ecosystem services for people (Kareiva and Marvier 2012). Others disagree (Soulé 2013). Some have claimed that nature is fine or improving (e.g., Lomborg 2001) and been savaged for it (e.g., Pimm and Harvey 2001). Others hope that technological change and urbanization will solve environmental problems (e.g., Brand 2010), whereas still others maintain that the expansion of cities (e.g., McDonald RI et al. 2008) and globalization of extractive technologies (e.g., Ehrenfeld 2003) will devastate what nature remains. Many (perhaps most) have just reduced their expectations. For them, conservation has become the art of slowing declines, stabilizing selected populations in intensely managed situations, and simply preventing the total extinction of species. After all, the best status any species can currently achieve on the International Union for Conservation of Nature's Red List is to become a Species of Least Concern.

We believe that a more useful discussion about the future of nature follows from defining the human conditions that will allow nature to recover, casting the present moment in light of long-term socioecological change. We suggest that lasting conservation success can best be realized when (a) the human population stabilizes and begins to decrease, (b) extreme poverty is alleviated, and (c) the majority of the world's people and institutions act on a shared belief that it is in their best interest to care for—rather than destroy—the natural bases of life on Earth.

Drawing reasonable inferences from current patterns, we can predict that a hundred years from now, the Earth may be inhabited by between 6 and 8 billion people, very few of whom live in extreme poverty, 70%–90% of whom live in towns and cities, and nearly all of whom participate in a globalized, market-based economy. It is not inconceivable that two centuries from now, the population could be half what it is today and the long-cherished goals of a world where people respect and care for nature may be realized, especially if we act now to foster this eventuality. We argue that these gains might be accomplished not through draconian population policies or ongoing perpetuation of poverty, but rather through the social dynamics of cities. Success is by no means inevitable, but as others have observed (e.g., Ausubel 2000), acting to accelerate these dynamics now offers the best opportunity humanity will ever have to recover nature on a global scale.

A recent study of how the human footprint has changed between 1993 and 2009 provides a quantitative indicator of these changes (Venter et al. 2016). The *human footprint* (*sensu* Sanderson et al. 2002) is a cumulative spatial index of population, land use, access, and energy consumption. Researchers found that although the human population grew 23% and the economy grew 153% in monetary terms, the effect on land use globally, as was measured by the mean human-footprint score, increased by only 9% over that period. They also showed that the fastest growth in human-footprint score was in middle-income countries, with some of the wealthiest countries experiencing slight decreases in average human influence. These studies show that even as human pressure on the environment has increased, it was not uniform nor in proportion to the population growth and economic activity that presumably are the ultimate drivers of human impact on nature. How can that be?

Here, we explore the interrelationships between demographics, economic growth, lifestyle, and human influence on nature. First, we illustrate the historically unique scale of current changes in population growth, poverty alleviation, and urbanization and present projections of these phenomena into the future. Second, we argue for the primacy of urbanization as a driver of change in demographics, resource consumption, and ideation and, in turn, develop a qualitative model of how changes in those factors drive environmental impacts, harming and then potentially helping nature in a broadly predictable way. Finally, we suggest how conservationists should reorient their efforts in the twenty-first century, given the constraints and opportunities of the transition from the "bottleneck" to the "breakthrough."

Three global trends relevant to conservation

Fundamental aspects of human life on Earth are changing rapidly in the twenty-first century, with profound consequences for biodiversity conservation. Here, we review three of them: the progress of the demographic transition, declines in poverty, and the pace and scale of urbanization.

The end of population growth. Everyone alive today has grown up in a world of expanding global population, as have our parents and our grandparents (figure 1a). We expect the population of the world to grow, and that expectation of growth influences how people conceive of the future of the economy, politics, and conservation. The surprise is that although modern populations continue to expand, the rate of population growth has been falling since the 1960s (figure 2a). There is broad agreement among demographers (e.g., Scherbov et al. 2011, UN DESA 2015, KC and Lutz 2017) that the world population, while continuing to grow in the interval, will stabilize around or shortly after 2100 at between 6 and 12 billion human beings (most likely 8 to 10 billion), although the exact timing and the height of the peak are unclear (figure 2b, 2c; see Gerland et al. 2014, Lutz et al. 2014). The different trajectories of future population, while all speculative, depend on deterministic

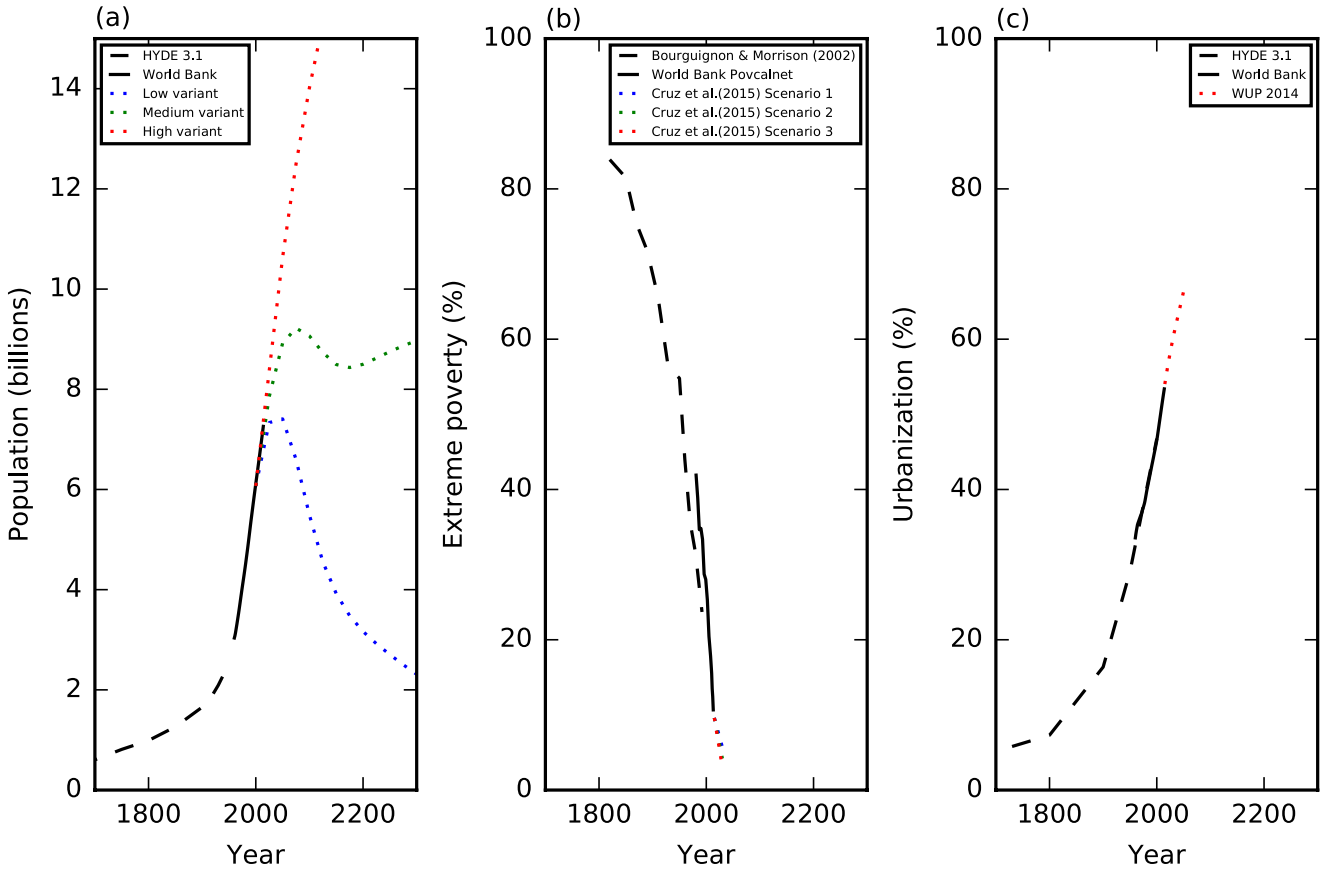

Figure 1. Long-term trajectories in (a) human population, (b) rates of impoverishment, and (c) urbanization. The population trends are from the years 1700–1950 (Goldewijk et al. 2010), 1960–2014 (World Bank 2016b), and 2015–2300 (UN DESA 2004); this includes low, medium, and high variants (see also figure 2b). The poverty estimates are from the years 1820–1992, the percentage of people living on less than $1.00 per day, adjusted for inflation (Bourguignon and Morrisson 2002); 1981–2015, the percentage living on less than $1.90 per day, using 2011 international dollars (World Bank 2016b); and 2015–2030, the percentage of people living on less than $1.90 per day, using 2011 international dollars (Cruz et al. 2015). **Urbanization,** ***defined as the proportion of the population living in towns or cities, are from the years 0–1950 (Goldewijk et al. 2010), 1960–2014 (World Bank 2016b), and 2015–2100 (UN DESA 2014). The historical reconstructions and future projections are dotted to indicate that they are estimates, whereas more recent data are estimates based on compiled census and economic surveys.***

or probabilistic simulations, which in turn depend on assumptions about the future trajectory of fertility, mortality, trade, and internal and external migration (KC and Lutz 2017).

The phenomenon of population growth and predictions of its eventual stabilization are explained by the well-known theory of the *demographic transition* (Notestein 1945). In brief, this theory holds that for most of history, human mortality and fertility rates were relatively high and approximately equal. Death was tragically frequent, especially among children. As a result, overall population growth was slow and sporadic, where progress was measured over centuries rather than decades. Estimates compiled by Livi-Bacci (2012) have suggested that between 10,000 BCE to the year 0, the global population grew from approximately 6 million people to some 252 million, at an annual growth rate of 0.037%. Between 0 and 1750 CE, the population grew almost 50% faster—but still slowly by modern standards—to about 771 million people globally (figure 1a).

These low-growth circumstances—the first stage of the demographic transition—began to change after 1750 in Europe, as medical advances in preventing and treating infectious diseases and public investment in hygiene began to curb the mortality rate (Dyson 2010). Whereas formerly, towns and cities were population sinks sustained by rural-to-urban migration, improvements in medical practice and urban governance (addressing issues such as sewage disposal, garbage removal, and provision of clean water) helped curtail deadly infectious diseases and enabled urban and rural populations to grow. In the second

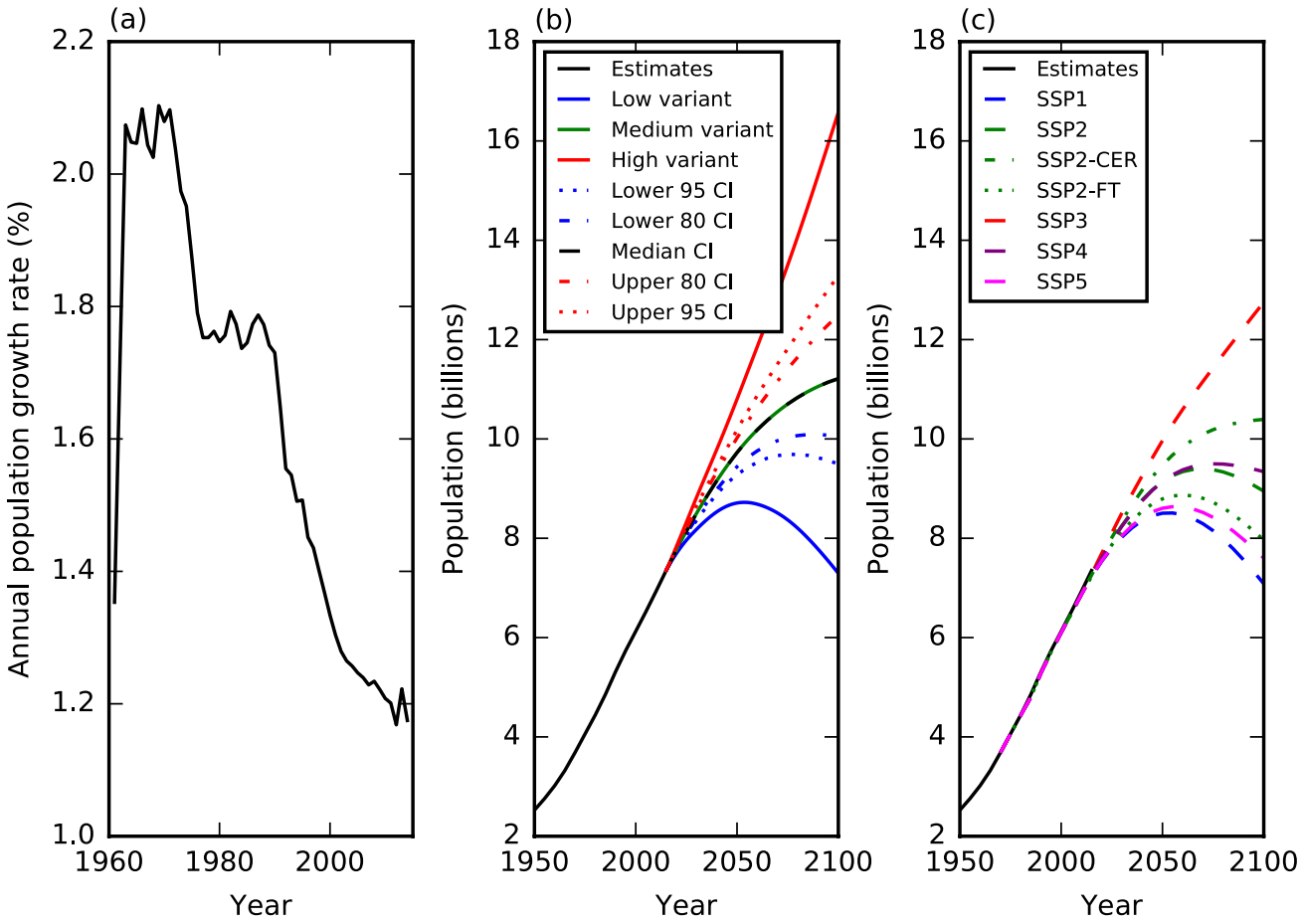

Figure 2. The changing trajectory of the global human population in terms of (a) annual population growth rate in 1960–2014 (World Bank 2016b); (b) deterministic high, medium, and low variants and probabilistic confidence of intervals of future total population in 2015–2100 (UN DESA 2015); and (c) scenario-based projections (KC and Lutz 2017) for shared socioeconomic pathways (SSPs). The UN deterministic projections are based on a long-term total fertility rate of 2.1 children per woman (medium variant), 2.6 children per woman (high variant), and 1.6 children per woman (low variant.) SSP1 assumes investments in health, education, and urbanization to spur the demographic transition, with moderate increases in fertility in developed countries, low-fertility trajectories elsewhere, and medium rates of migration between countries. SSP2 assumes "middle of the road" assumptions about future changes in mortality, fertility, migration, and education. SSP3 assumes a divided world of low migration, low fertility in developed countries, and high fertility in developing ones. SSP4 assumes high inequality between and within countries, leading to differential education attainment, continued fertility trends as present, and medium migration. SSP5 assumes technological investments that lead to high education and low mortality, with higher fertility in developed countries and low fertility elsewhere, and high levels of migration. See O'Neill and colleagues (2017) for additional details about the SSPs.

stage of the demographic transition (sometimes described as a *demographic revolution*; McEvedy and Jones 1978), lower mortality coupled with high levels of fertility led to burgeoning populations. In England and Wales, for example, the population from 1750 to 1800 grew from 6.1 million to 9.1 million, followed by a doubling to 18 million by 1850 and another near doubling to 33 million by 1900 (McEvedy and Jones 1978). Similar trends—although each having their own historical trajectories—have been documented for France, Germany, the Netherlands, and European Russia in the nineteenth century and slightly later for Japan, China, India, and Indonesia. The United States, Australia, Canada, New Zealand, Brazil, and Argentina have demographic histories that combine rates of natural increase with the receipt of immigrants from other parts of the world. This historical period of unprecedented growth, coupled with urbanization, produced the crowded, polluted cities described so memorably by Charles Dickens, Victor Hugo, and others. Analogous processes of internal and international migration coupled with population growth continue to create vast slums in the developing world today (UN Habitat 2013).

Eventually, as European, American, and more recently, Asian nations became more urban and developed, fertility rates began to drop, reaching rates on par with mortality and effecting population stabilization, albeit at much higher population numbers than in the pretransitional times. In the early twenty-first century, most of the world population is experiencing this third stage of the demographic transition, led by trends in China and India. Some of the advanced economies have passed to a fourth, arguably "post-transitional" stage, at which fertility drops below mortality rates, creating the potential for, if not the actuality of, absolute population declines (e.g., in Japan, Hungry, Portugal, and Lithuania; see UN DESA 2015).

Because population is a compounding phenomenon, over the long term (i.e., decades to centuries), small differences in net population dynamics make large differences in total population size. Illustrative in this regard are speculative long-term projections from the UN Population Division (UN DESA 2004) through 2300 (figure 1a). They produce three variants of population projections, of which the medium variant is most often cited. The medium variant includes an assumption that over the long-term, individual countries will equilibrate in the postdemographic transition at the "replacement rate," at which a woman over the course of her lifetime will have, on average, 2.1 children. The medium variant leads to a prediction that the world population will peak around 9.1 billion people shortly after 2100 and then float at approximately 9 billion ever after. The high variant assumes a long-term total fertility rate of 2.6 children per woman, which leads to 36.4 billion people by 2300, an estimate that greatly exceeds population levels supportable by current agricultural patterns (Sayre 2008). The most optimistic projection is the low variant, which assumes a total fertility rate of 1.6 children per woman, a level in keeping with the current fertility rates in developed economies but on a worldwide scale. Remarkably, were such fertility patterns sustained, they would lead to a world of 2.3 billion (not 9 billion–10 billion) by 2300.

Policy-relevant *shared socioeconomic pathways* (SSPs)—developed by O'Neill and colleagues (2017) based on scenarios of health, education, and international migration through 2100 (figure 2b)—show how startling divergent twenty-first-century demographic pathways could be. A world where international migration, trade, and development assistance are limited could lead to a world of 12 billion by century's end (SSP 3; KC and Lutz 2017). The best-case scenario reflects ongoing investments in health, education, and cities, which could lead to a twenty-second-century Earth with a population below 7 billion (i.e., a population smaller than today; SSP 1).

The end of poverty. The world today is much wealthier than it ever was. As with population growth, reconstructions by Maddison (2007) have suggested that for most of recorded history, economic growth was so slow as to be barely noticeable, on order of 0.1% per year. It was only with the Industrial Revolution that economies began to grow significantly. Developing countries—such as the United Kingdom in the early nineteenth century, the United States in the late nineteenth and early twentieth century, or China more recently—have economies that can grow at 5%–8% annually before maturing to still-significant but lower growth rates (1%–3% per annum; De Long 1988).

The tremendous wealth generated in the Great Acceleration has not been evenly shared across countries or within them. Much has been written about disproportionate gains made by the richest people and countries, increasing levels of inequality (e.g., Piketty 2014). Less remarked on but also important is how economic growth has benefited people at the lowest end of the income scale, both individuals and nations as a whole (table 1). In 1981, more than half of the population of the developing world lived on less than $1.25 a day; by 2010, that proportion had fallen to 21%, despite a 59% increase in the developing world's population (Olinto et al. 2013). Chandy and Gertz (2011) estimated that increased economic growth in middle- and low-income countries over the last three decades has helped some 721 million people escape extreme poverty (approximately 24 million fewer poor per year). In East Asia and Pacific countries, the rate of rural poverty declined by threefold between 1990 and 2008 (Cruz et al. 2015).

Recent gains in poverty alleviation appear to be driven by people migrating from the countryside to towns and cities or by urban areas expanding to incorporate nearby rural areas (Angel 2012, Turok and McGranahan 2013). Most economists see rural-to-urban migrations driven by economic opportunity and other benefits of urbanization (Glaeser 2011)—so-called pull factors—whereas others note that some migrations are also driven by antagonistic land-use policies and climate change (Davis 2007)—that is, push factors.

The economic effects of people living closer together in urban agglomerations are ubiquitous. Per capita incomes increase dramatically with urbanization of society (Glaeser 2011, Turok and McGranahan 2013). "Spillover" economic effects can help rural incomes as well by providing markets for goods and direct transmittances of cash (Christiaensen et al. 2013). Inducements to inhabit urban agglomerations seem to prevail even over living conditions, because many poor rural-to-urban migrants find themselves living in slums in terrible conditions, often in peri-urban areas. As we noted above, poor living conditions were commonplace in European and North American cities well into the twentieth century, until the provision of clean water, urban sanitation, and decent housing made possible gains in health and welfare, setting the stage for more sustainable urban forms.

Even though the World Bank recently moved the poverty threshold from $1.25 to $1.90 per person per day (Ferreira 2015), the global poverty rate still may have fallen to single digits by 2015, and predictions suggest that by 2030, the

Table 1. The share of the extremely poor by region, in which poverty is defined as earnings less than $1.25 per day, based on 2005 purchasing power parity data.

Years:	1990		1996		2002		2008	
Regions	**Rural**	**Urban**	**Rural**	**Urban**	**Rural**	**Urban**	**Rural**	**Urban**
East Asia and Pacific	67.5	24.4	45.9	13	39.2	6.9	20.4	4.3
Europe and Central Asia	2.2	0.9	6.3	2.8	4.4	1.1	1.2	0.2
Latin America and the Caribbean	21	7.4	20.3	6.3	20.3	8.3	13.2	3.1
Middle East and North Africa	9.1	1.9	5.6	0.9	7.5	1.2	4.1	0.8
South Asia	50.5	40.1	46.1	35.2	45.1	35.2	38.0	29.7
Sub-Saharan Africa	55	41.5	56.8	40.6	52.3	41.4	47.1	33.6
Total	**52.5**	**20.5**	**43**	**17**	**39.5**	**15.1**	**29.4**	**11.6**

Source: World Bank and IMF (2013).

percentage of the extremely poor could be between 3%–7% globally (figure 1b; Cruz et al. 2015). Although over 700 million people globally are still poor, including many living in sub-Saharan Africa, the international adoption of sustainable development goal 1 ("End poverty in all forms everywhere") suggests a realistic aspiration to what only a few decades before seemed an impossible ambition: the eradication of extreme poverty.

The growth of cities. Cities are changing, too (figure 1c). Between 1950 and 1990, the number of people living in urban areas increased from approximately 746 million to 2.29 billion; between 1990 and 2014, urban populations grew again by another 1.6 billion people, an addition equal to the entire world population of 1900. Urbanization over the next 35 years is expected to add another 2.5 billion people to the world's towns and cities (UN DESA 2014). Longer-term projections range from 55% to 90% of all people living in towns and cities by 2100 (Jiang and O'Neill 2017).

All regions of the world have urbanized over the last 100 years (note the progression of data with respect to the *x*-axis in figure 3). Most developed countries currently have urbanization levels that exceed 70%, including Western Europe, Japan, Canada, and the United States. Latin America and the Caribbean is the most urbanized region in the world, with urbanization percentages of 70%–80%. Although the United Nations does not have a single, standard definition of an urban place and allows each country to use its own definition (UN DESA 2014), the prevailing pattern is clear. It is important to note that most definitions include not only large megacities and heavily built-up places (e.g., Manhattan and central Tokyo) but also smaller towns, including suburbs, which house many more people worldwide than skyscraper-filled central business districts (Christiaensen et al. 2013).

As is apparent to the more than 50% of humanity that lives within them, urban agglomerations have expanded outward at unprecedented rates over the last 100 years, with the areas of land urbanized growing even faster than the urban populations (Angel 2012). Most experts believe this trend will continue. Güneralp and Seto (2013) predicted that between 2000 and 2030, global urban land cover will grow by 200% while urban populations will grow by some 70%. However, collectively, urban areas occupy only a relatively small fraction of the Earth's surface. Examining different measures of urban extent, Seto and colleagues (2011) estimated that urban areas covered 0.2%–2.7% of global land area in 2000 and evaluated growth scenarios that suggest a maximum extent of 5.9% by 2030.

Urbanization and biodiversity conservation in the Anthropocene

Now, we turn from these extraordinary trends to observations about how urbanization affects all of them, using the IPAT framework to organize our discussion in terms of population, affluence (and therefore, consumption), and technology (or more broadly, ideation). In economics and sociology, *urbanization* is often described as yet another characteristic of development, along with technological innovation, industrialization, trade liberalization, and good governance, all of which contribute to rising per capita incomes (e.g., Jones 2013). Environmentalists have traditionally seen urbanization as mainly about the movement of rural people to urban areas, driving increases in consumption and therefore concerns about environmental impact (e.g., Rees and Wackernagel 1996). We argue that both of these views have distracted conservationists from the critical effects of urbanization on the choices people make about how to live.

Urbanization as a driver of change in population, consumption, and technology. Although advances in medical science and hygiene are generally accepted as decisive for the declines in mortality during the demographic transition, the causes for the "fertility transition" have been long debated by demographers (Dyson 2010). The most credible recent explanations seem to be tightly interwoven with urbanization (Mace 2008, Martine et al. 2013). As we discussed

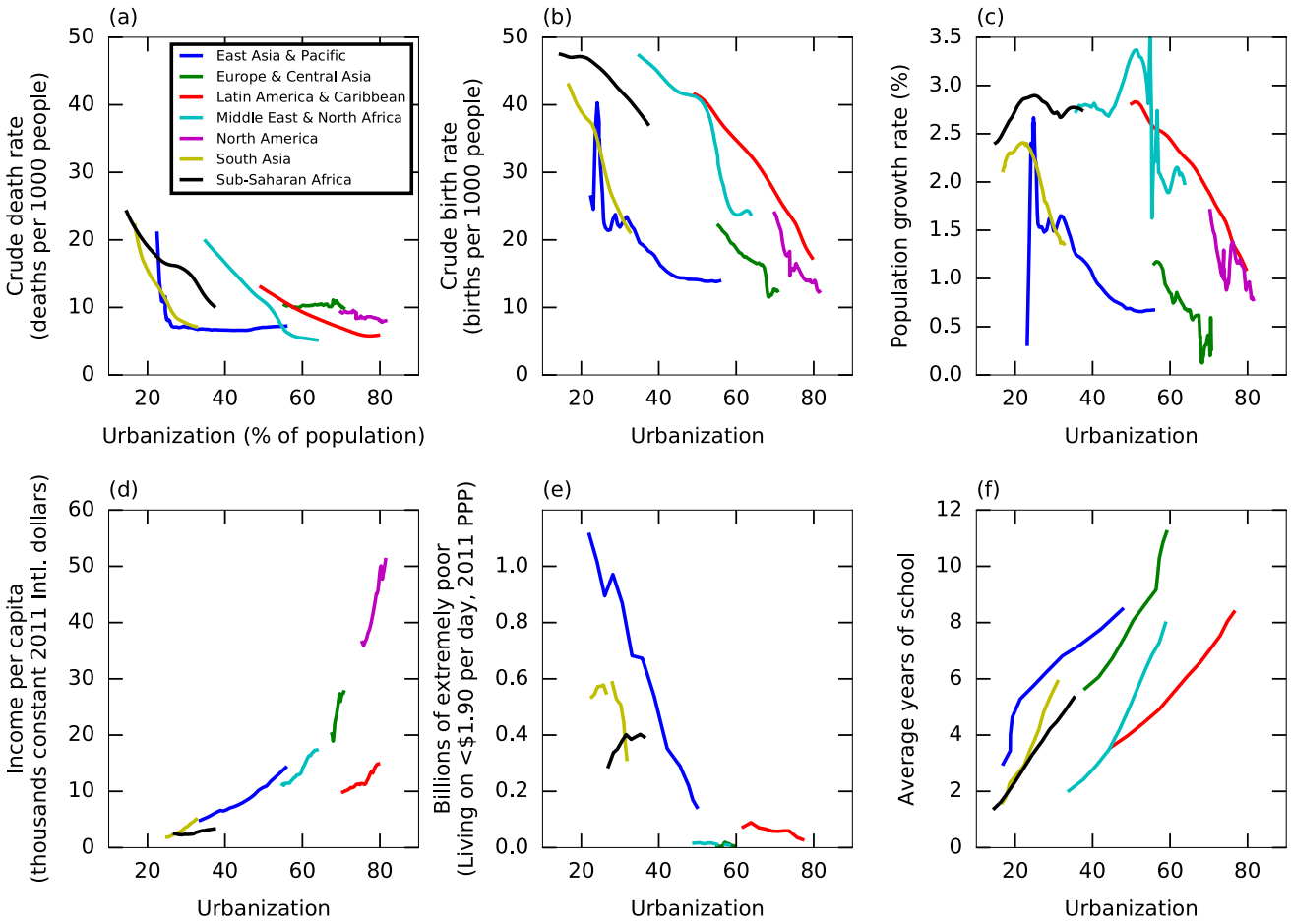

Figure 3. Demographic and social trends plotted against urbanization in 1960–2014, after Angel (2012). Each plot shows average values for countries in regional groupings as defined by the World Bank (2016b): (a) crude death rate (deaths per 1000 people); (b) crude fertility rate (births per 1000 people); (c) annual population growth rate (percentage); (d) income per capita (in constant 2011 international dollars); (e) number of people living on less than $1.90 per day (in constant 2011 international dollars); and (f) average years of schooling (including primary, secondary, and tertiary school) for people over 15 years old. All data are from the World Bank (2016b) except those for panel (f), which are from Barro and Lee (2016). Note that the poverty data in panel (e) include only developing countries in those regions and exclude North American countries entirely.

above, when people live in cities, they have a better chance to find employment in diversified economies, which allow individuals to better exploit their particular skills and predilections. Simultaneously, urban economies tend to be larger because of agglomeration effects, which create more, better-paying, and diverse jobs than in rural economies. Increased opportunities for work lead to greater autonomy, especially for women, who gain more control over their reproductive lives, in part through access to contraception, family planning, and education (Lutz and Qiang 2002) and in part through the changing cultural norms and power dynamics that result from women holding more income of their own (McDonald P 2000). Because urban families experience higher costs for rent, food, and other necessities, without the offsetting benefits that greater labor from children provides in agricultural economies, incentives for large families diminish as people move to town (Notestein 1945). Also, in cities, people have better access to medical care, which means that life expectancies improve, which further implies that couples have less reason to hedge against infant mortality with additional births (Mace 2008). Because urban kids will likely become urban adults working in skilled, nonagricultural jobs, education is incentivized (Maralani 2008). The effects are clear in the data: Plotting World Bank–compiled statistics on mortality and fertility rates against urbanization shows precipitous declines, with mortality followed by fertility (figure 3a, 3b). The net result is that population growth rates have also declined for all regions of the world except sub-Saharan Africa (figure 3c).

Regional per capita incomes have also increased with urbanization (figure 3d), resulting in dramatic reductions in extreme poverty, most notably in East Asia (figure 3e), and improvements in education attainment (figure 3f). Environmentalists often assume that consumption necessarily increases with income, so urbanization must also drive higher consumption, but the relationship between income and consumption is more nuanced. For the very poor becoming slightly less so, each new increment of income is likely to be spent; as economists describe it, their marginal propensity to consume is high (close to one). But as overall wealth increases, other options for income beyond immediate consumption become available, including savings ("deferred consumption") and spending less time working and more time at leisure (Nicholson and Snyder 2011). As John Maynard Keynes observed in 1936, "The fundamental psychological law… is that men [and women] are disposed, as a rule and on average, to increase their consumption as their income increases, but not as much as the increase in their income." The practical effect is that the relationship between income and consumption is nonlinear, often assumed to be logarithmic (e.g., Jones 2013), with a tendency to flatten at higher incomes as the marginal utility of consumption declines. As poor people become wealthier, it is true that they will consume more as they fulfill their basic human rights to healthy food, adequate clothing, and decent housing. But as people become wealthier still, their immediate consumption may not—and generally is not—in proportion to their increased disposable income; they can and do make other choices with their time and money.

Empirical studies have shown that urban people consume different goods and services than rural people. A panel from the World Consumption Database (World Bank 2016a) for 12 megadiverse countries (*sensu* Mittermeier et al. 2005) demonstrates, not surprisingly, that urban consumers spend more than rural ones, whether in Madagascar or the United States (table 2). But it also shows that urban people typically spend proportionally less on food and more on housing, transport, and financial services than rural people. Consumption of meat and processed foods increases with urbanization, increasing the environmental impact and health consequences of diet (Reardon et al. 2014). Housing costs more for smaller spaces in town, which decreases the per capita physical footprint of inhabitation and lowers shared infrastructure costs, such as sanitation, water supply, electricity, and schooling, leading to environmental advantages of urban lifestyles or rural ones (Sanderson 2013). Density is inversely correlated with energy consumption for transportation because density makes shared transportation modes more desirable and travel distances shorter (Newman and Kenworthy 1999).

As populations urbanize, most goods and services are purchased in markets, which increasingly draw on national and international supply chains. These "over-the-horizon" economic relationships displace the environmental costs of consumption (Ehrenfeld 2003). Although globalization distributes threats to biodiversity, it is important to recognize that globally interconnected urban economies also enlarge and diversify the markets in which people choose what they consume and where and how it is sourced. These decisions, if informed by education, regulation, economic policy, or social norms, can lead to the dematerialization of consumption, "decoupling" natural-resource extraction from economic growth (UNEP 2011, although see Ward et al. 2016).

Collectively, these urban economic relationships translate into improved welfare at lower environmental cost for urban lifestyles over rural ones at equivalent levels of income. Dudwick and colleagues (2011) in a global survey comparing urban and rural consumers reported that "on average, urban areas enjoy a higher standard of living than rural areas… though there is a high level of variation." Studies of consumption in New York City indicate that the average New Yorker consumes 74% less water, uses 35% less electricity, and produces 45% less garbage per person when compared with the average American (City of New York 2011). Cities, of course, use enormous amounts of resources and generate tremendous quantities of wastes, but their environmental advantages are revealed when consumption statistics are reported on a per capita basis (Meyer 2013).

Fair and transparent urban governance seems to be particularly important in determining how efficiently towns and cities deliver these benefits to their constituents. London and New York had difficulty cleaning up their local environments and creating healthy living conditions until they stemmed the grossest extremes of political corruption through nineteenth- and early-twentieth-century political reform movements. Potts (2009) and Kessides (2005), among others, have seen a similar condition in sub-Saharan Africa today, where urbanization has not translated into the same economic or demographic benefits that other regions have experienced (figure 3c–3f). Interestingly, controlling graft was also highlighted by Venter and colleagues (2016) as a factor influencing why economically growing countries have differential human-footprint outcomes between 1993 and 2009; lower corruption scores and greater urbanization percentages were associated with decreased human influence at the national scale. Unrest can also unhinge the relationship between urbanization and other social goods, as has been shown recently in the Middle East and North Africa (Serageldin et al. 2014).

Finally, we note briefly that urban places are hubs of ideation and technological development, including ideas such as conservation. Given good governance, health, safety, and amenable circumstances, people working in close proximity generate new ideas, rapidly innovate and iterate, and have the capital and interconnectivity to deploy improvements widely (Glaeser 2011). Historically, cities have been centers of arts, science, and communication, developing everything from writing and religion to electric engines and the automobile (Sanderson 2013). Recent work has shown how new patent applications, economic activity, and even the pace at which

Table 2. A comparison of annual average per capita consumer expenditures in rural and urban settings in 12 biologically megadiverse countries (sensu Mittermeier et al. 2005) in or around 2010. The consumption sectors accounting for 10% or more of annual expenditures are shaded.

			Expenditures in each sector (%)											
Nation	Setting	Per capita expenditure	Food and beverages	Housing	Clothing and footwear	Water	Energy	Appliances, etc.	Transport	Education	Health	ICT	Financial Services	Other goods and services
Brazil	Rur	2,789	28	6	6	1	5	2	25	2	8	2	<1	15
	Urb	4,527	23	6	6	1	5	2	24	4	8	3	<1	18
Colombia	Rur	1,524	50	17	4	<1	5	NA	8	<1	6	3	2	5
	Urb	4,174	33	21	4	1	3	NA	10	2	6	5	8	8
China	Rur	1,141	42	11	6	1	5	<1	5	7	7	7	1	10
	Urb	3,549	34	5	10	1	5	<1	6	7	8	9	1	13
Democratic Republic of Congo	Rur	218	75	<1	6	1	5	1	1	2	3	<1	NA	6
	Urb	374	63	4	5	2	6	2	4	4	4	2	NA	5
India	Rur	597	55	2	7	<1	9	3	5	2	5	3	<1	10
	Urb	1,364	35	23	5	<1	7	2	6	5	4	4	<1	9
Indonesia	Rur	767	55	8	4	<1	6	2	8	2	2	2	<1	11
	Urb	1,269	45	14	3	1	5	2	10	4	2	4	<1	10
Madagascar	Rur	210	68	10	5	<1	2	<1	5	1	1	<1	NA	7
	Urb	457	57	15	4	1	6	<1	5	3	1	2	NA	6
Mexico	Rur	1,404	28	23	7	1	5	7	11	6	3	3	<1	5
	Urb	3,037	22	27	6	1	4	6	9	9	2	5	1	9
Papua New Guinea	Rur	2,821	72	7	2	<1	<1	<1	2	2	4	1	<1	11
	Urb	5,484	57	11	3	<1	<1	1	3	5	5	1	<1	14
Peru	Rur	1,415	49	10	6	<1	2	2	12	1	6	5	<1	6
	Urb	3,489	30	20	5	1	4	3	12	2	6	8	<1	9
Republic of South Africa	Rur	1,598	27	19	7	1	4	2	17	1	1	4	9	9
	Urb	5,467	13	26	4	1	4	1	18	3	1	4	15	10
United States	Rur	16,617	14	28	3	NA	NA	NA	20	1	8	NA	10	15
	Urb	19,667	13	34	4	NA	NA	NA	16	2	7	NA	11	13

Source: Total expenditures are provided in purchasing power parity adjusted international dollars, based on 2005 purchasing power parity statistics, from the World Bank's Global Consumption Database (World Bank 2016a), except for US data, which is from Hawk (2013), which reported household expenditures (we assumed a household size of 2.56 persons per household to convert to per capita expenditures).
Abbreviations: ICT, Information and communications technologies; Rur, rural; Urb, urban.

people walk scale superlinearly with city size (Bettencourt et al. 2007). Cities are also the places where many social movements begin (Nicholls 2008), including campaigns to conserve nature and natural resources. As an example, our organization was founded in 1895 in New York City with the goal to save wildlife and connect New Yorkers to nature. Many other conservation organizations have been founded in cities, including the first Audubon Society (New York City, New York, 1886), the Royal Society for Protection of Birds (Manchester, United Kingdom, 1889), the Sierra Club (San Francisco, California, 1892), The Nature Conservancy (Arlington, Virginia, 1951), Greenpeace (Vancouver, British Columbia, 1971), and Conservation International (Washington, DC, 1987). Many rural residents care deeply about and contribute vitally to conservation efforts, but it is difficult to imagine the long-term success of conservation without also enlisting the support, creativity, and collective power of the more than half of the world's population who live in towns and cities (Rees and Wackernagel 1996, Sanderson 2013).

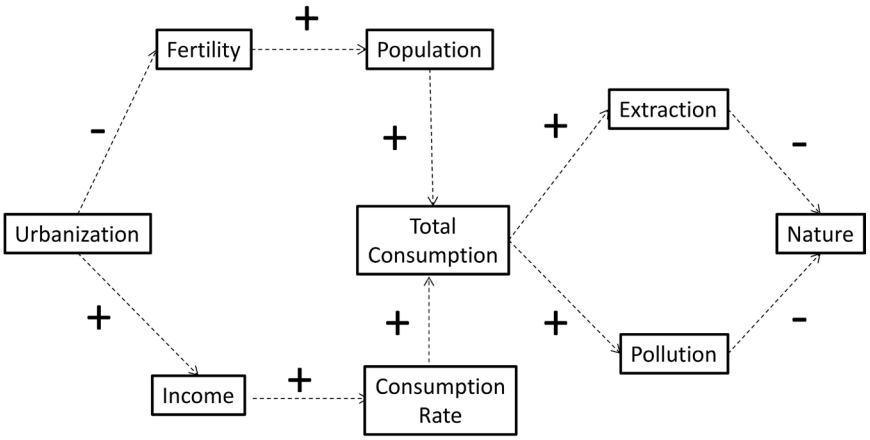

Figure 4. A conceptual framework connecting demographic and economic trends in the twenty-first century to impacts on the environment. Urbanization is considered a key driver that increases incomes and decreases fertility over time. Fertility increases population, income enables higher consumption rates, and population and the consumption rate multiplied together and summed over the population increase the total consumption of a society. Consumption is satisfied through economic production processes that typically generate pollution and motivate natural resource extraction, both of which have negative impacts on aspects of nature, characterized by species, ecosystems, and ecosystem-function declines. During the twentieth and early twenty-first centuries, population and income have both been rising, driving consumption and dramatic declines in nature. Eventually, however, if populations stabilize and perhaps decrease (figure 2) and the relationship between income and consumption moderates (figure 5b), then one can imagine the prospect of lesser impacts on nature and therefore more positive prospects for conservation and restoration of nature. This theory accounts for the bottleneck of pressures nature has experienced over the last few hundred years and suggests a possible breakthrough when pressures relax in the future—dependent, of course, on the national and international policies that countries choose to employ. Not shown are the effects of cities on ideation and technological development, which can either enhance or diminish rates of extraction and pollution, depending on sociocultural values and incentives.

From bottleneck to breakthrough. Figure 4 presents a causal-chain diagram connecting urbanization to biodiversity impacts through demographic and economic intermediaries. On the left side of the figure 4, urbanization acts to decrease fertility and increase income, as we discussed above. Income, in turn, is positively correlated with consumption rates, and the product of per capita consumption rates and population, summed across all individuals in society, equals total consumption.

Aggregate consumption drives declines in nature through two parallel mechanisms on the right side of figure 4. Human use of natural resources requires extracting materials from ecosystems, either by removing biomass (e.g., logging, hunting, and fishing) or withdrawing abiotic elements (e.g., water, minerals, and fossil fuels). At industrial scales, these processes drive whole-scale conversion of natural ecosystems into managed ones that are more productive for people. Extraction affects species either through direct competition (i.e., harvesting plants or animals) or indirectly by diminishing the natural resources wild species need (e.g., water and habitat). Human activities also generate waste materials released back to the environment. Pollution can render habitats toxic to people and other species, altering ontogenies, increasing mutation rates, and/or contributing to mortality, and pollution can alter abiotic cycles, as in anthropogenic contributions to climate change. Technology (not shown) acts as a mediating factor, either increasing or decreasing environmental impacts, depending on how it is incented and deployed.

Figure 5 provides schematic expressions of four key relationships, helping to explain how the framework described in figure 4 is changing in the Anthropocene. First, conservationists need to recognize that the demographic transition, which for nearly all of human history has operated to increase population, is now working toward population stabilization, although the pace and speed are contingent on national and international policy (figure 5a). If investments continue to be made in human welfare, particularly health, education, and female empowerment, especially in sub-Saharan Africa, then populations may begin to peak midcentury and decline by century's end (KC and Lutz 2017). Second, as incomes increase, so does consumption, but the relationship is not linear at all levels of income: Savings, work–leisure tradeoffs, satiation, consumer choices, and technological decoupling can contribute to a flattening (if not a leveling) of per capita consumption with greater incomes (figure 5b). Third, as societies urbanize, there is a shift in the agents of natural-resource extraction (figure 5c). Rural people, especially poor rural people, are more likely to supply their subsistence needs for food, water, and fuel through their own efforts, whereas urban people are more likely to supply their economic needs through the marketplace. Market choices are sensitive to price signals and other considerations (e.g., environmentally friendly labeling, celebrity endorsements, and taxation) in a way that household extraction for subsidence is not. So although it is abundantly clear that environmental impacts increase as societies move through the demographic transition and urbanize, the ongoing fertility transition and poverty alleviation resulting from urbanization suggest the prospect for eventual stabilization and long-term declines in overall environmental impacts (figure 5d).

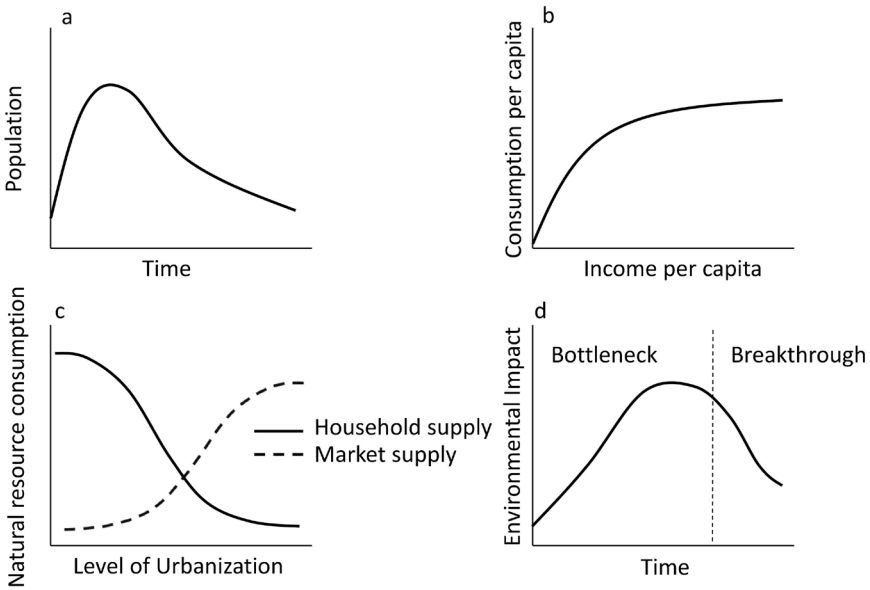

Figure 5. Four key relationships underlie the bottleneck and breakthrough theory described in the main text. Panel (a) shows the peaking and decline of population over time, reiterating the relationships in figure 2. Panel (b) shows that consumption increases linearly as people move out of poverty and then flattens out, following approximately a logarithmic trajectory, based on conjectures about the changing marginal propensity to consume as incomes increase. Panel (c) shows that as populations urbanize, the effects on natural-resource extraction move from direct actions of people on nature to indirect effects mediated by the marketplace. Figure (d) expresses the prediction that the long-term effects of urbanization will cause human impact on nature to peak and then decline. Although each country and region will find its own path through these relationships, we expect that by 2100, most of the world will have passed through the current bottleneck into a breakthrough period of conservation, although the exact form of that passage depends on policy interventions and conservation investments in the meantime.

These relationships (figures 4 and 5) predict a prolonged bottleneck period of heightened pressure, followed by a breakthrough period characterized by the release of pressures on species and ecosystems, enabling nature to recover (figure 5d). Others have posited a similar future history. Nordhaus and Shellenberger (2007) coined the term "Break Through," amplifying what Ausubel (2000) earlier called the "Great Reversal." Blomqvist and colleagues (2015) referred to this bottleneck period as "peak global environmental impact." Where our argument differs from these others is its emphasis on urbanization (Sanderson et al. 2017). Urbanization leads; population stabilization, poverty alleviation, economic transformation, and new ideas follow; and in their wake, the prospects for biodiversity improve.

Because urbanization proceeds at different rates in different regions, there will not be a single global bottleneck but many—not one universal breakthrough but thousands, happening in different places at different times, with local reverses and sudden gains to be expected. The speed and trajectory of the transitions depend on the many factors that influence demographic and economic transformation, especially the pace and mode of urbanization. Nevertheless, the power of the trends described above suggests for all regions and for the world as a whole the same eventual results: populations stabilized, absolute poverty banished, and the opportunity for new notions about the human relationship to the Earth advanced.

Implications for twenty-first-century conservation practice

At the core of our argument is the seemingly contradictory statement that the mechanisms that are destroying nature are laying the foundation for its long-term recovery. Passing through the bottleneck is necessary to reach the breakthrough. The conservationist's paradox is that the same forces that are destroying nature now are also creating the circumstances for long-term success. The conservationist's challenge is to keep the bottleneck open wide enough so that nature can survive to a breakthrough.

Achieving a stable human population will require a net increase in total consumption as all people move out of poverty and follow the common trajectory of investing more in smaller families, for which they have greater security. Reaching a world with 6 billion people and vast natural expanses necessitates investing to make cities healthy, safe, and amenable for people, not just because they concentrate people into a smaller space, but also because of the ways in which urbanization influences social mobility, wealth creation, female empowerment, and ultimately, fertility. Developing a broadly shared environmental consciousness about nature is predicated on an unimpoverished, largely urbanized world that shares the positive externalities of education, technology, and, indeed, nature conservation.

The profound danger is that by the time the foundations of recovery are in place, little of wildlife and wild places will be left. If society focuses only on economic development and technological innovation as a mechanism to pass through the bottleneck as fast as possible (*sensu* Brand 2010), then what remains of nature could well be sacrificed. If society were to focus only on limiting economic growth to protect nature (*sensu* Meadows et al. 2004), then terrible poverty and population growth could overwhelm what remains. Either extreme risks narrowing the bottleneck to such an

Table 3. The bottleneck and breakthrough theory has important implications for conservation practice in the twenty-first century. Here, we propose how conservation operates during the bottleneck period of a country or region's development, when pressures are increasing, and how conservation might evolve once pressures have begun to stabilize and eventually decrease after the breakthrough.

Conservation during bottleneck	Conservation after the breakthrough
Protect threatened elements of biodiversity	Restore surviving elements of biodiversity
Establish protected areas as bastions of the wild	Manage protected areas as source sites for rewilding
Leverage rural-to-urban migration to reshape threats to biodiversity and reduce poverty	Leverage urban-to-rural support for conservation
Contribute to safe, livable, and sustainable cities	Deconstruct infrastructure that is no longer needed
Enact regulation to limit destructive natural-resource extraction and pollution	Enact economic measures to shape consumption

extent that our world passes through without its tigers, elephants, rainforests, coral reefs, or a life-sustaining climate. Therefore, the only sensible path for conservation is to continue its efforts to protect biodiversity while engaging in cities to build the foundations for a lasting recovery of nature.

To illustrate some of implications of this theory, we contrast conservation during the bottleneck to conservation after a breakthrough (table 3). A country or a region can be said to be caught in the bottleneck for as long as its population is growing and rates of total natural-resource extraction and pollution are increasing. Analogously, a country or region begins the breakthrough when populations stabilize and natural-resource extraction and pollution rates begin to decline in absolute terms.

During bottleneck periods, conservation needs to continue to identify and protect threatened elements of biodiversity (Soulé 2013). The most effective tool in our toolkit remains well-funded, socially inclusive, competently managed protected areas, which place legal limits on destructive activities. Breakthrough conservation suggests over time adjusting the management of protected areas, conceiving of these areas less as bastions against ever-mounting threats and more as source sites (*sensu* Walston et al. 2010) for restoring and rewilding continents and oceans. The expansion of large wildlife in Europe provides a trenchant example (Chapron et al. 2014).

Rural-to-urban migration presents a dilemma for conservation. Because many protected areas are in less-populated, low-governance areas that are important for conservation, rural residents and indigenous groups are often the only bulwark against destructive actors (e.g., industrial logging, large-scale agriculture, and criminal activity). But for many rural people, a route out of poverty may be to move to nearby towns or distant cities and away from remote parks and reserves. Where local people are the best stewards of nature, conservationists should continue to rely on community-based approaches to deliver benefits for nature and people (Naughton-Treves et al. 2005). In other circumstances, recognizing that people living in remote regions dependent on natural resources are often among the world's poorest, most politically marginalized, and most market isolated, conservation organizations may need to assist with voluntary relocations (Karanth 2007) that in the long run are better for people and nature and employ other forms of pragmatic conservation management (Robinson 2011).

Cities must be central to any global conservation strategy, because urbanization is the only lever that that simultaneously shifts populations, alleviates poverty, and spurs innovation, which individually and in combination have the potential to alter resource extraction and pollution, as we discussed above. The tremendous demographic and economic effects of urbanization have been demonstrated in all regions of the world except sub-Saharan Africa, which may be the exception that proves the rule. Improving the governance and functioning of African urban areas while simultaneously protecting Africa's unique wildlife is arguably the most urgent need in conservation today, because it is the fastest path to global population stabilization. Moreover, well-governed, inclusive, livable cities in Africa and elsewhere give conservationists the potent platform we need to activate new, broad-based conservation movements (e.g., Asafu-Adjaye et al. 2015)—what Nordhaus and Shellenberger (2007) have called a *politics of possibilities*. Conservation needs cities to work for nature.

But nature also needs to work for cities. Highlighting the role of cities in biodiversity conservation may seem counterintuitive, even ironic, because the expansion of built-up areas itself is a significant ecological concern (McDonald RI et al. 2008, Güneralp and Seto 2013). Urban development disrupts hydrological and nutrient cycles, destroys and fragments habitat, concentrates pollution, and provides portals for the introduction of invasive species (Grimm et al. 2008). Recognizing these impacts, many efforts are underway to mitigate them through green infrastructure, land-use planning, restoration, and place-based education. Increasingly, these activities are informed by new developments in urban ecology, conservation biology, and resilience science (Pickett et al. 2011). Urban conservation activities make towns and cities not only less destructive to nature locally but also more attractive to immigrants and residents, who will appreciate the benefits of local nature and whose lifestyle choices can provide benefits to nature elsewhere.

Because urbanization creates and relies on a global market economy, the best way to influence urban consumption and innovation is through economic decision-making (i.e., prices). Directly costing in negative environmental externalities (*sensu* Pigou 1920) will force markets to address them in all phases of production, from resource extraction through transport and production of finished goods to release of pollution and wastes back into the environment. Because nature does not charge for the ecosystem services it provides, pricing these externalities is a matter of public policy, which can be addressed through a wide variety of financial as well as regulatory mechanisms, such as carbon taxes, land-value assessments, and/or various forms of ecological-use fees (Sanderson 2013).

Finally, our theory suggests a new way to articulate the future of conservation and attract more of society to the cause. The immediacy of the threats encapsulated by "planetary boundaries" and related lines of catastrophic thinking are not only devastating to contemplate but may also be shortsighted. The world does not end in 2050, as too many data graphs do. Nor is environmentalism dead, despite claims to the contrary. Rather, if the demographic and economic phenomena that we discuss here do come to pass, it means that conservation faces another 30–50 years of extreme difficulty, when more losses can be expected. However, if we can sustain enough nature through the bottleneck—despite climate change, growth in the population and economy, and urban expansion—then we can see the future of nature in a dramatically more positive light. Much as the eighteenth-century Enlightenment created the conditions for our world, we need a twenty-first-century Renaissance of wisdom, founded on the belief that our role as human beings is to restore, steward, and celebrate the Earth's unique and immanent nature.

Conclusions

Thinking about the future of conservation is both humbling and challenging, especially as it has been formulated in the Anthropocene. The underlying demographic processes, although massive, are slow moving compared with the cycles of government, funding, and careers in conservation. To be seen clearly, these trends require a historical perspective that is difficult to adopt if one is focused on immediate threats and captivated by apocalyptic futures. But there is hope. Like in London during the Blitz, vigilance and exertion are required, but we need not panic or despair because the weight of history is on our side.

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